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Order GRUIFORMES

Diverse assemblage of small to very large wading and terrestrial birds. Morphologically diverse, with few unifying characters within the Order. Anatomical details are summarized by Sibley & Ahlquist (1990). Possibly polyphyletic, though DNA comparisons indicate that the Order is monophyletic, composed of highly divergent groups that are more closely related to one another than to members of any other order (Sibley & Ahlquist 1990). The boundaries of the Order and relationships with other Orders and between families in this Order are uncertain (Sibley 1960; Sibley & Ahlquist 1972, 1990; Cracraft 1973; G.F. van Tets).

Peters, Wetmore (1960) and Storer (1971) recognized 12 families: Eurypygidae (monotypic Sun-bittern of tropical America); Otididae (bustards); Gruidae (cranes); Heliornithidae (finfoots of tropical Old and New World; three monotypic species); Aramididae (monotypic Limpkin of tropical and subtropical America); Psophiidae (trumpeters of tropical America; three species in single genus); Cariamidae (seriemas of central S. America; two monotypic genera); Rhynochetidae (monotypic Kagu of New Caledonia); Rallidae (crakes and rails); Mesitornithidae (mesites of Madagascar; three species in two genera); Pedionomidae (monotypic Plains-wanderer of Aust.); and Turnicidae (button-quails).

The Plains-wanderer is now recognized as being a charadriiform on evidence of morphology (Olson & Steadman 1981) and DNA-DNA hybridization (Sibley *et al.* 1988). Sibley *et al.* (1988) and Sibley & Ahlquist (1990) placed the Turnicidae in a separate Order, the Turniciformes *incertae sedis* (which we follow here; q.v.) and included Aramididae within the Heliornithidae but otherwise retained a similar arrangement of families. The Mesitornithidae, Rhynochetidae and Otididae have also been regarded as separate Orders.

Only Gruidae, Rallidae and Otididae occur in our region; other families are not considered further here.

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Family RALLIDAE rails, crakes and gallinules

A group of small to medium-sized (12–65 cm long), generally slender, terrestrial birds, usually of wetlands, often very secretive and skulking. Almost cosmopolitan, not occurring in polar regions and waterless deserts. In our region, 17 breeding species in 11 genera, five accidentals (one doubtful) and three extinct. Relation to other Gruiformes not fully resolved; skeletal morphology suggests close alliance to Psophiidae (trumpeters) and Heliornithidae (sungrebes) (Cracraft 1973); Aramididae, Eurypygididae and Cariamididae of S. America, and Rhynochetidae of New Caledonia and the extinct Aptornithidae of NZ also closely related; some or all of these families could be included as sub-families in Rallidae (G.F. van Tets). DNA–DNA hybridization evidence shows Rallidae form a distinct cluster separate from cranes and their allies (Sibley & Ahlquist 1990). Olson (1973b) recognized two sub-families: the monotypic Himantornithinae and the Rallinae, with Himantornithinae intermediate between Rallinae and Psophiidae. The Jacanidae (Charadriiformes; q.v.) may be derived as aquatic specialists from *Gallinula*-like stock and more appropriately placed within the Rallidae (G.F. van Tets).

Arrangements within the Rallidae have varied: Peters recognized 52 genera; Thomson (1964), 45; Olson (1973b), 35; Ripley (1977) 17; BWP, 32–39; Campbell & Lack (1985), 18; and Sibley & Ahlquist (1990) 34 (142 species). Rallidae vary anatomically in relation to diet and habitat. Olson (1973b) suggested they evolved from terrestrial to aquatic but admits evolution may have occurred several times. For practical purposes, broad division often made into (1) rails, crakes and wood-rails, most of which are terrestrial (in HANZAB region: *Rallina*, *Gallirallus*, *Dryolimnas*, *Porzana*, *Eulabeornis*, *Crex*); and (2) coots and gallinules (including swamphens, native-hens and waterhens), which tend to be more aquatic (in HANZAB region: *Amauromis*, *Gallinula*, *Porphyrio*, *Fulica*, *Gallicrex*). The affinities of the genera and, in brackets, the number of volant and flightless species recorded in HANZAB region given below. *Rallina* (2, 0): one species occurring Aust. and New Guinea and another vagrant to Aust.; close relatives are *Canirallus* and *Sarothrura* of Africa, *Mentocrex* of Madagascar and *Rallacula* of New Guinea (Olson 1973b). *Gallirallus* (1, 4): widespread in Indo-Pacific region; one or more species of volant *Gallirallus* are thought to be ancestral to several insular species in the sw. Pacific, including *lafresnayanus* of New Caledonia and *sylvestris* of Lord Howe I. (Olson 1973b; Fullagar & Disney 1981; Schodde & de Naurois 1982; Diamond 1991). *Dryolimnas* (1, 0): one species (*pectoralis*) occurring Aust. and Auckland Is; closely related to *Gallirallus* and *Rallus*; *pectoralis* often placed in *Rallus*. *Amauromis* (1, 0): one species occurring Aust., New Guinea, Philippines and Moluccas. *Porzana* (5, 0): worldwide, with four species native to our region and one vagrant; we follow Mees (1982) by including *Poliolimnas* in *Porzana*; Olson (1973b) thought *Porzana* may have evolved from *Amauromis*. *Eulabeornis* (1, 0) endemic to n. Aust. and Aru Is, and according to Olson (1973b), an allopatric close relative of *Habroptila* (1, 1) of Wallacea and New Guinea. *Crex* (1, 0) breeds in Eurasia and migrates S, mainly to Africa; vagrant to Aust. and, doubtfully, to NZ. *Gallicrex* (1, 0): vagrant from se. Asia to Christmas I. (Ind.); may also have derived from *Amauromis*. *Gallinula* (2, 1) worldwide distribution, with three species in our area; also an *Amauromis* derivative; sub-genus *Tribonyx* is endemic to Aust. with a fossil record going back to Pliocene (Olson 1975); differ from *Gallinula* in broad bill, long tail and short toes. *Porphyrio* (2, 2) appears to be a *Gallinula* derivative, with sub-genus *Porphyryla* intermediate in shape and plumage between *Gallinula* and nominate *Porphyrio* of Africa, Asia and Aust.; the sub-genus *Notornis* of Lord Howe I. and NZ consists of obvious derivatives of the nominate, but are terrestrial with an exceptionally deep bill and short toes. *Fulica* (1, 0): worldwide distribution, with one species in our region, and two flightless extinct species in NZ; probably derived from *Gallinula*-like stock (Olson 1973b).

Bodies, short, often laterally compressed for ease of movement in dense vegetation. Neck, short or moderately long; 14–15 cervical vertebrae. Males, often slightly larger than females. Wings, short, broad, rounded; in volant species, flight appears low, weak and generally not sustained though some species capable of long-distance movements, occurring on or colonizing oceanic islands (e.g. Purple Gallinule *Porphyrio martinica*, Watercock *Gallicrex cinerea* in HANZAB region). Some island species are flightless, yet many others migrate or disperse over long distances. In HANZAB region, all species have 11 primaries (p11 minute) and 10–12 secondaries; in Family, 10–20 secondaries, smaller species have ten and some flightless species have fewer primaries (BWP); diastataxic. Short sharp curved claw on alula. Tail, short, square to rounded, soft; often raised or flicked up to signal colours of under tail-coverts; normally 12 (6–16) rectrices. Bill varies: often rather slender, straight and slightly longer than head, and in some species, slightly decurved; or quite short and laterally compressed (crakes, most gallinules, coots); or massive and laterally compressed (some species of *Porphyrio*). Gallinules and coots have smooth, plate-like horny frontal shield (continuous with ramphotheca) on forehead. Nostrils usually in large depression (not in *Porphyrio*), pervious and perforate in some species. Sense of smell said to be well developed (Ripley 1977). Legs, well developed, usually strong, long to quite short, often laterally compressed. Toes, long and slender but may be rather short and heavy; hind toe, large, slightly raised. In most gallinules (not native-hens *Gallinula*, Takahe *Porphyrio mantelli* and White Gallinule *P. alba*) and some crakes, toes greatly elongated and legs modified for walking on floating vegetation; in coots, toes have enlarged lateral lobes to aid swimming, and pelvis and legs modified for diving. All species can swim; dive easily and can sink, using wings under water if necessary. Many species climb easily among thick vegetation; downy young of some (and

possibly adults) use wing-claw to assist climbing. Oil-gland bi-lobed, feathered in most species. Caeca, long. Syrinx, simple; tracho-bronchial. Feathers, fairly loose and soft, frayed and even hair-like in some; small after-feather usual.

Plumage, generally sombre browns, chestnut, black, or greys; iridescent purplish-blue and green in *Porphyrio*. Barring on flanks common. Vent and under tail-coverts may contrast with rest of plumage. Upperparts, spotted, barred, streaked, or plain. Bare parts often brightly coloured and forehead shield conspicuous. Sexes usually similar or nearly so (except in *Sarothrura* and *Gallixrex*). Pre-breeding moults restricted or absent, with no seasonal changes in appearance (except in *Gallixrex*) but colours of bare parts change in some species, coinciding with moults. Post-breeding moult, complete. Remiges may be moulted irregularly, or simultaneously, with consequent flightless period. Post-juvenile moult partial; can be followed by partial pre-alternate moult or by complete second pre-basic. Young, downy, and unlike other precocial birds, black (sometimes iridescent) or dark brown, which may be an adaptation for hiding in dense vegetation; evidently a derived condition (Olson 1973b). In some species, downy young have brightly coloured bills or skin on head or both, which may function for signalling (Fjeldså 1977). Downy young of *Gallinula*, *Porphyrio* and *Fulica* also have white or yellow terminal bristles on down. Post-natal development slower than in some other precocial birds, such as Galliformes and Turniciformes, with initial emphasis on development of legs and feet and not wings; flight-feathers develop last. Juveniles generally similar to but duller than adults.

Numerous flightless forms; incidence of flightlessness perhaps greater than in any other group except ratites and penguins. Flightlessness has evolved many times within the Rallidae, often and repeatedly on islands without predators and probably independently each time; appears to evolve rapidly and so probably of little phylogenetic significance above the level of species (Olson 1973a). Selection reduces flight-muscle and pectoral girdle, possibly through neoteny (Olson 1973a); usually corresponding increase in development of leg muscles. Frequency of flightlessness suggests that rails are predisposed to it; they are certainly pre-adapted for coping with some of the restrictions it imposes: many volant species are behaviourally flightless, e.g. avoiding predators by running away; many are temporarily flightless during wing-moult (a feature shared with several other groups containing flightless forms), when secretive and elusive; and post-natal development of flight is slow. In many species, populations of insular flightless species exterminated by introduced predators (e.g. Chatham Island Rail *Gallirallus modestus*, Dieffenbach's Rail *Gallirallus dieffenbachi*). Subfossils from our region have been reviewed (Olson 1977) and include flightless and often large species of coot, waterhen, rail and wood-rail and the distinctive snipe-rail *Capellirallus*. For discussion of biogeography of *Gallirallus* see Olson (1973b), Fullagar *et al.* (1982), Schodde & de Naurois (1982), and Diamond (1991).

Most inhabit all sorts of terrestrial, estuarine and littoral wetlands, from sea-level to mountain highlands. Some genera found in lowland and montane forests; others in wet grasslands; still others, e.g. Takahe *Porphyrio mantelli*, *Crex*, tussock grasslands, hay-fields and similar places, not necessarily with wet areas. Some species migratory; many dispersive; others apparently sedentary. Patterns of movements in HANZAB region generally not known, perhaps because they appear to take place at night and perhaps because the birds are so secretive and silent when not breeding that absences may be more supposed than real. Gallinules and coots appear to be more sedentary than crakes and rails, though at least the Black-tailed Native-hen *Gallinula ventralis* is notably irruptive, in response to floods and droughts of inland Aust.

Omnivorous, or in some species mostly vegetarian. Species with long thin bills probe for invertebrates in soft ground and litter. Eat all sorts of plants and submerged vegetation, insects, molluscs, crustaceans, eggs and young of other birds, small fish and carrion. Some gallinules graze, e.g. Tasmanian Native-hen *Gallinula mortierii* and coots. Only *Fulica* dives for food; they and *Gallinula* will up-end. Often wash food in water.

Mostly solitary or in small groups, though densities can be very high in some wetlands; *Gallinula* (e.g. Black-tailed Native-hen *Gallinula ventralis*) and *Fulica* form large flocks, especially in winter; after onset of inland droughts, irruptions may involve thousands of birds. Roost solitarily except in species that flock; generally at night on ground in cover; occasionally in bushes and trees. Some species nocturnal or crepuscular. Most species nest solitarily; some strongly territorial, advertising territories with loud persistent calling and chasing of intruders. Dense vegetation and apparently secretive habits make it hard to study social organization and behaviour in most species. Agonistic and sexual behaviour often conspicuous with wing-spreading, tail-flicking, fighting with use of bill and feet and other ritualized features of display. Pair-bond usually monogamous and only for one season but may be sustained. Polygyny known in captivity and suspected in wild, e.g. in *C. crex*; polyandry occurs in Tasmanian Native-hen *Gallinula mortierii* and possibly Weka *Gallirallus australis*. Co-operative breeding in some gallinules, e.g. Dusky Moorhen *Gallinula tenebrosa*. Pair-formation and courtship little known except in some gallinules and coots, in which a variety of chasing, bowing, nibbling, mock-preening and feeding, and courtship feeding takes place; no elaborate ceremonies at time of nest-relief. Copulation and other activities take place out of water or on specially built platforms. Most species very vocal, with screams, trills, whistles, booms, rattles, trumpets, grunts or barks; can be ventriloquial; mostly silent when not breeding but social species have loud rallying cries. Stand at rest (sometimes on one leg) in hunched posture with head sunk on shoulders, or lie down; sleep with head on back and bill among feathers. Bathe in shallow water, alternately ducking head in water and flipping water over back or by beating half-open wings in water; coots may bathe while swimming. Leave water to oil and preen after bathing. Sun themselves after preening. Allopeening common. Scratch head directly. Some species (e.g. *Porphyrio porphyrio*, *P. alba*, *P. mantelli*) recorded manipulating and grasping food in foot or holding down large items with feet.

Breed seasonally and protractedly. Nest fairly deep and cup-shaped; in some rails, domed; in wetlands, often with ramps up to nests. In thick vegetation, often near or on surface of water but some species nest high in trees; use old nests of other birds or nest on ground far from water; materials from any available plants; built by both sexes. Horned Coot *F. cornuta* of S. America builds islands of small stones. Some build nests that float or are attached to aquatic vegetation; nests on water may be built up rapidly if water-level rises. Non-functional nests often found in gallinules and *Gallinula*, which also build nursery nests after young hatch. Eggs, blunt oval; smooth and fairly glossy; dull white to tan ground-colour, blotched and spotted red-brown to black; unspotted in *Rallina*. Clutch-size, 5–10 (1–18) but dump-laying or laying by more than one female in same nest may complicate estimation of size of clutch laid by an individual. Usually one or two broods and replacement layings up to three times. Lay at intervals of 24 or 48 h. Incubation usually by both sexes but in some by female alone or with only small share by male. Incubation period, 14–24 days per egg; start of incubation varies from first to last egg and so hatching synchronic or asynchronic. Egg-shells left in nest or removed. Generally have two large lateral and one small median brood-patches. Young hatch in down, precocial, nidifugous; at first fed bill to bill, becoming self-feeding within few days or not until 8 weeks old. Normally tended by both parents and, in a few species, offspring of previous broods may help to feed young, e.g. *Gallinula*, occasionally *Porphyrio*. Fledging period, 30–60 days (20–70) and then independent except in co-operative breeders. First breeding usually when 1 year old or less.

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Porphyrio mantelli Takahe

Notornis mantelli Owen, 1848, *Trans. zool. Soc. Lond.* 3: 347, Pl. 56, figs 7–13 — subfossil skull from near Waingongoro, North Island, New Zealand.

Named in honour of Walter Baldock Durant Mantell (1820–95), British amateur geologist and naturalist who lived in New Zealand; founder and secretary of the New Zealand Institute and President of the Wellington Philosophical Society.

POLYTYPIC Nominate *mantelli*, extinct, NI, NZ; *hochstetteri* Meyer, 1883, SI, NZ.

FIELD IDENTIFICATION Length 63 cm; stand c. 50 cm tall; weight: male 2.7 kg, female 2.3 kg. Largest rail in HANZAB area; thickset, flightless, with colourful plumage, massive bill and frontal shield, and robust and powerful legs and feet; wings reduced. Much larger and more robust than Purple Swamphen *Porphyrio porphyrio*. Sexes alike, males slightly larger. No seasonal variation. Juvenile separable.

Description Adult Plumage loose with silken sheen. Head and neck, iridescent dark bluish-purple, merging into paler bluish-purple mantle. Rest of upperparts and most inner wing-coverts, olive with varying blue iridescence; remiges, primary coverts and outer greater secondary coverts, dark bluish-purple. Underbody, iridescent dark bluish-purple, grading to paler bluish-purple on axillaries and sides of upper breast; under tail-coverts, white. Frontal shield and base of bill, red; rest of bill, pinkish red to reddish. Iris, brown to reddish brown. Legs and feet, pinkish to pinkish red. **Juvenile** Similar to adult but duller; head and neck, brownish grey; chin, throat and face varying mottled white; upperparts have no blue iridescence and become brown with wear; underparts, dull purplish-blue, with brownish tinge at first. Bill and developing frontal shield, almost black except for small white tip to upper mandible (begin to develop adult colour before post-juvenile moult); iris, dark brown to grey; legs and feet, horn to dark purplish-brown.

Similar species None; hardly likely to be confused with **Purple Swamphen**, which is much smaller, with smaller bill, longer legs and can fly. Calls easily confused with those of *Weka Gallirallus australis* but generally deeper and more resonant.

In pairs or small family groups in alpine tussock grasslands; also subalpine scrub and beech forests in winter. Active throughout day and sometimes well into night. Gait and posture like Weka, flick tail continuously when nervous; when alarmed, break into surprisingly fast run with head and neck lowered and wings used to gain impetus, quickly disappearing into cover. Rarely venture into water but can swim. Contact call an almost monosyllabic rising squawk; often given in answer to similar though disyllabic and rather more flute-like call of Weka; also utters single monotonous crow and, when alarmed, a deep resonant boom.

HABITAT Grassland and forest, though before decline may have included coastal sand-ridges and open shrubland (Reid 1974a). Now confined to c. 650 km² of Murchison Mts in Fiordland; in area of heavy snows and very high rainfall, 2500–4800 mm per annum (Williams 1952; Reid 1971; G. Rasch; J.A. Mills). At present, commonly above tree-line, 1050–1520 m asl (Falla 1949; Reid 1969b; Reid & Stack 1974; DOC in press).

Throughout mountainous country in Murchison Mts (Williams 1952, 1960; Mills 1976). When snow covers alpine tussock grassland, birds found in subalpine scrub or lower in beech

forest (Reid 1969b; Mills *et al.* 1984). Alpine grassland dominated by snow tussocks *Chionochloa*, c. 1 m high; with sedges *Carex*, *Schoenus*, short grasses *Festuca*, *Poa*, herbs *Celmisia*, *Aciphylla*, and shrubs *Hebe*, *Coprosma*, *Olearia*, *Dracophyllum* (Lavers & Mills 1984; DOC in press); the Takahe Valley and Point Burn areas dominated by Red Tussock *C. rubra* and less preferred habitat; above the tree-line, *C. rigida amara*, *C. pallens*, and *C. crassiuscula* predominate (Mills 1974b; Mills & Lavers 1974). Forest dominated by Mountain Beech *Nothofagus solandri* and Silver Beech *N. menziesii* (Turbott 1951; G. Rasch; J.A. Mills); understory of shrubs (*Coprosma*), ferns (*Hypolepis*, *Blechnum*), and hookgrass *Uncinia* (Mills 1977). Where introduced on islands, in pastures of exotic grasses, e.g. Prairie Grass *Bromus willdenowii*, Yorkshire Fog *Holcus lanatus* and clovers *Trifolium*, and Cocksfoot *Dactylus glomerata* (D. Eason).

Frequent mountain lakes, rivers, streams, bogs (Falla 1949; Fleming 1951; Williams & Miers 1958; Reid 1974a); often by swiftly flowing streams (Williams 1960). Some areas prone to flooding (Anon. 1952; Reid 1971). Vegetation includes sedges and rushes (e.g. *Juncus gregiflorus*) (Mills *et al.* 1980). Wade, swim and dive (Falla 1949; Turbott 1951; Riney & Miers 1956).

Forage on tussock grassland when not covered by deep snow; otherwise on forest floor (Reid 1969b; Mills 1976). Availability of rhizomes affected by depth of snow and degree of freezing of soil (Mills 1977). Nest on well-drained ground among tussocks (Falla 1949; Reid 1969b). Chicks and adults hide in vegetation (Riney & Miers 1956). Will shelter in forest and under bluffs during winter (Williams 1960; Mills *et al.* 1980).

DISTRIBUTION AND POPULATION Endemic to NZ; restricted to Fiordland. Formerly widespread NI and SI. Recently introduced to several nearshore islands.

NZ SI Mainly in Murchison Ra.: arms of the Middle Fiord of L. Te Anau, possibly extending N to Stuart Ra., S to Kepler Ra., and between George and Caswell Sounds in the W, where sightings are less numerous (Reid 1969b; Mills 1974b; Falla *et al.* 1981; Lavers & Mills 1984; Oliver; NZRD). **Breeding** Throughout range.

Introductions Introduced to four nearshore islands that are mainly free from predators: Tiritiri Matangi I.: three adults and one egg from Maud I., May 1991–Aug. 1992. Kapiti I.: unsuccessful introduction one captive pair and one wild pair, 1968–71 (Reid 1977); ten captive birds, 1989 (three temporarily relocated from Mana I.), July 1989–July 1991. Mana I.: nine birds (three to Kapiti I.), Sept. 1988–June 1992. Maud I.: twelve (four relocated), Apr. 1984–June 1990. Have bred successfully on all four islands; island population, 29 (DOC in press)

Subfossil in Maori middens throughout NI and SI (Reid 1974a; Lavers & Mills 1984; NZRD). Four specimens collected in nineteenth century (Dusky and Thompson Sound, 1849, 1851, s.



L. Te Anau, 1879–98) (Falla 1949). Later unconfirmed records in first half of twentieth century from Milford Sound to Preservation Inlet, and E to Waiiau R. (Falla 1949; Cumming 1953; Reid 1974a; Mills 1976; Lavers & Mills 1984). However, was thought to be extinct by 1930s. Rediscovered W of *L. Te Anau*, 20 Nov. 1948 (Falla 1949) and then probably distributed within 750–800 km² (Reid 1971). Range contracted between 1948 and 1966

mainly on w. edge where the species disappeared from several valleys (Reid 1971; Mills 1976) but also from Wapiti region and Kepler Ras (Lavers & Mills 1984). By 1966, occupied c. 600 km² (Reid 1971; Mills 1973, 1974b, 1976).

Rare. Population at time of rediscovery probably c. 260 pairs (Reid 1971), though this may be over estimate (DOC in press). Between 1948 and 1966, population slowly declined to 180–200 pairs, while declines of up to 2% per year were recorded in w. part of range; in e. and central part, populations stable (Reid 1971; Mills 1973). From 1967 to 1973, numbers in e. Murchison Ra. steadily decreased (Mills 1973; Lavers & Mills 1984). In mid-1950s, adult population in Point Burn and Takahe Valley c. 50 birds (Williams & Miers 1958); between 1963–64 and 1971–72, the number of adults recorded in this area fell from 47–50 to 19–23, the number of occupied territories declined from 20 to 10 (see Table 1, Reid 1971). In 1974, total wild population estimated to be 200 pairs in c. 650 km² of Fiordland NP (Mills 1975). Total wild population in 1980, c. 120 birds (Lavers & Mills 1984). By 1991, population 260 (Anon. 1991). Since then, numbers have fluctuated between 120 and 180 (DOC in press).

Introduced Red Deer *Cervus elaphus* have modified habitat by grazing (see Habitat); also, as their diet overlaps with that of Takahe, the two compete for food. Although Deer usually eat different parts of tussocks from that eaten by Takahe, severe competition arises from overgrazing by Deer, which eliminate most nutritious plants (Mills 1976, 1977; Mills *et al.* 1989). Grazing by Deer may prevent some grasses from seeding, thus reducing another source of food (Williams 1952). Intense culling has now reduced Deer (Mills 1976; Lavers & Mills 1984).

Captive breeding at Mt Bruce Native Bird Reserve since 1950s has had little success; fertile eggs were not produced till 1972; few chicks have survived to independence (Reid 1977; Lavers & Mills 1984). Since 1987, methods have improved, with 90% of viable eggs hatching and 74% of chicks raised to maturity ($n=117$ viable eggs, 1982–91) (Eason 1992).

MOVEMENTS Sedentary; flightless. Hold territories from Oct. to May; held through winter until snow prevents feeding, when descend into forest or scrub (Reid 1969b; Mills 1973; Mills & Fowler 1979; Mills *et al.* 1980); in winter some wander 5–10 km from grassland territories; possibly up to 30 km (Reid 1974a; DOC in press). Seasonal pattern of movement within territories: when breeding (Oct.–Dec.), inhabit low- and mid-altitude zones of grassland (1000–1100 m asl) irrespective of snow cover at higher altitudes; in mid-Dec. found at higher altitudes (up to c. 1500 m asl) where preferred food plants grow (Mills *et al.* 1991; DOC in press). Long movements occur usually in winter and early spring when food scarce (Williams 1952). Temporary immigra-

Table 1 Breeding populations in Murchison Mts, 1963–72 (Reid 1971), and 1972–74 (Mills & Lavers 1974).

	1963–64	64–65	66–67	67–68	Year 68–69	69–70	70–71	71–72	72–73	73–74
No. of adults										
(a)	47–50	45–48	43–46	36–39	26–28	22–24	18–22	19–23	17	14
(b)									44	41
(c)									30	38
No. of pairs										
(a)	3–7	11–14	14–17	9–10	5–7	3–4	5–6	6–7	8	6
(b)									19	20
(c)									12	19

(a) Takahe Valley and Point Burn, 10.5 km²; (b) Eyles-Wisely, 36.3 km²; (c) Miller Peak, 18.1 km².

tion of adults recorded 1972–73 in Takahe Valley and Point Burn district; birds remained till at least mid-Apr. (Mills 1974b; Mills & Lavers 1974). May move farther as chicks become mobile (Williams & Miers 1958); recorded moving 400–800 m within few days of hatching (Riney & Miers 1956). Known to move across and between valleys, especially juveniles (Riney & Miers 1956; Williams & Miers 1958). Last century four specimens taken at low altitudes during severe weather (Reid 1974a).

Banding Maximum movement from natal or breeding territory is 21 km, after loss of male (DOC in press). Birds in e. part of range move farther to find enough food because quality of habitat lower than in W (Mills 1976; Lavers & Crouchley 1985). Young may move greater distances than older birds, in search of territory or mate (Williams & Miers 1958). Of ten birds, banded as chicks in Takahe Valley and recaptured a year later, seven recovered in natal territory or with parents, one at edge of natal territory, one in neighbouring territory (about 1 km away), one with another adult (c. 2.5 km away). Of seven birds recorded 2 years after banding: one with parents, one on edge of natal territory, one moved c. 1.7 km, two moved to Point Burn (c. 2 and 2.7 km), both that moved in first year remained in same area. Of four recorded as 3-year-olds: one c. 3.2 km from where seen as yearling, another moved to Point Burn, two remained in valley of which one found c. 1.4 km from where hatched. Of 34 banded birds, five moved from Takahe Valley to Point Burn and 19 were not recovered (Reid 1967).

FOOD Mainly vegetarian; mainly leaf-bases of snow tussocks and other alpine grassland species, with grass seeds and fern rhizomes taken seasonally; rarely invertebrates and small reptiles.

Behaviour Information from contribution by DOC (in press) unless stated. Diurnal, though in winter will feed till 22:00. Pull tussock tillers out using bill, transferring to feet, where held parrot-fashion. Force of 15.5 kg required to break *Chionochloa* tiller at junction of stem and leaf sheath. Strip seeds from plant by running partly opened bill along flower stalk. Obtain seed-heads beyond reach by cutting stalk and stripping seeds while holding stalk in foot. Dig up rhizomes of ferns with beak. Selective feeders: take bases of plants with more nitrogen, phosphorus, potassium, calcium, sodium and soluble sugars. Adjust diet seasonally: as snow covers tussocks, move to beech forest where *Hypolepis* rhizomes make up to 80% of diet by late winter. Essentially extractors of plant juices, as food passes quickly through system with little fibrous material digested and plant tissue structurally unaltered. Adults and chicks ingest quantities of quartz grit to assist with grinding of food (Mills & Mark 1977; Mills *et al.* 1980, 1991).

Adult (Mills & Mark 1977; Mills *et al.* 1980; DOC in press): Plants: Pteridophyta: Hypolepidae: *Hypolepis millefolium* rhizomes (60–80% vol. winter); Juncaceae: *Juncus gregiflorus* bases (winter); Cyperaceae: *Uncinia affinis*, *U. calvata* and *Carex coriacea* leaf bases and rhizomes (all winter); *Schoenus pauciflorus*; Poaceae: *Chionochloa rigida amara* (8–34% vol. summer), *C. pallens* (25–75), *C. crassiuscula* (0–23), *C. teretifolia* (occasionally), *C. rubra* (all year, valleys and lowlands) *C. conspicua* leaf bases and seeds (winter); *Poa colensoi*, *P. novaezelandiae*, *Rhytidosperra setifolia* and *Festuca matthewsii* sds (annually); Apiaceae: *Aciphylla takahe* leaf bases, fl., sds, stems (especially Feb.–Apr.); Asteraceae: *Celmisia petriei* (18–48). Animals: invertebrates. On islands: leaf blades, leaf bases and seeds of many introduced grasses: including Cocksfoot *Dactylis glomerata*, Prairie Grass *Bromius willdenowii*, Timothy *Phleum pratense*, *Poa pratensis*, Yorkshire Fog *Holcus lanatus*, Brown Top *Agrostis capillaris*; leaves and bases of clovers *Trifolium*, especially Red Clover *T. rubra*; all parts of Chickweed *Stellaria media*; occa-

sionally dead sticks, grass and stalks of flax (R. Walters; D. Eason). Animals: invertebrates; small lizards (Maud I., T. Whitaker).

Young Depend on parents for food for 4 months as unable to pull out leaf tillers themselves; bases of *Chionochloa* and invertebrates fed to chicks from first day. Invertebrates large proportion of diet of chicks for 4–6 weeks; predominantly vegetarian by 6–8 weeks; ingest grit when less than 2-weeks old (Williams 1960; D. Eason). Adults turn over several square metres of vegetation searching for invertebrates, including larval, pupal and adult insects, spiders and worms (Gurr 1951; Williams 1960).

Intake Estimated 2.0–2.2 kcal/g/day needed (Reid 1974b).

SOCIAL ORGANIZATION Fairly well known; account based mainly on Mills (1975, 1978), Reid (1967, 1969a), Williams (1960), Williams & Miers (1958), Falla (1951), DOC (in press); contribution by G. Rasch and J.A. Mills; also in captivity (Reid 1977). Mainly in pairs or in family groups, but also solitary; in breeding season, c. 82% of adults appear paired, and c. 70% of pairs breed, but these figures vary between years (Reid 1967); largest family group seen, two 4-month-old chicks, two yearlings, and parents (DOC in press); in winter, family group maintains close contact (Mills 1975). Pairs hold territory when breeding, but at other times remain nearby in well-defined home-range (e.g. Williams 1960; DOC in press).

Bonds Monogamous; bond held all year, probably for life, and at least 12 years. If mate lost, tend not to lay in same season (Mills 1975) but will pair with new bird at earliest opportunity (D. Eason). Pair-formation and breeding usually occurs from 2-years old (Lavers & Mills 1984); on Maud I., pair of 1-year-old birds bred successfully (D. Crouchley); evidence of breeding in first-year in Fiordland (Williams & Miers 1958). Birds may pair but not lay in same season (Williams 1960). **Co-operative breeding** During breeding, juveniles sometimes evicted by parents; if remaining with parents, they help incubate occasionally, and feed and tend chicks (Lavers & Mills 1984; T. Hook; D. Eason). In captivity, multiple male helpers reported (Reid 1977). In captivity and on Tiritiri Matangi I., single sex pairs (male x male and female x female) have successfully hatched and raised chicks from fostered eggs, though some individuals in captivity will not tolerate another bird of the same sex (D. Eason). **Parental care** Both adults build nest; incubation shared equally between pair (Williams 1960 *contra* Falla 1951); both feed and brood chicks (Williams 1960; Lavers & Mills 1984). Young depend on parents for food for c. 4 months; remain with parents during winter, usually dispersing in following spring; some juveniles remain for up to 18 months (DOC in press), though Reid (1967) found 2-year-olds either in pairs, alone or still with parents. At first, subadults remain near natal territory but then drift away (Reid 1967); occasionally juvenile, expelled by parents in spring, remains on edge of territory in early breeding season, and accepted back into territory later in season (J.A. Mills). In captivity, hand-reared chicks successfully fostered by other adults, even males, and second year birds will foster small groups (6–10) of first year birds.

Breeding dispersion Population concentrated into loose colonies but, within these, solitary pairs defend secluded territories some distance from neighbours; young of last year often tolerated as helpers. In addition to egg-nests, territory may include trial- or brood-nests or both (Williams 1960). Sometimes only 2–3 pairs/valley (Reid 1969b); space available to each pair during nesting, 2.5–80+ ha, averaging 30–35 ha (Reid & Stack 1974) (also see Distribution). **Territories** Defended in breeding season by breeding and non-breeding pairs (Fleming 1951); all-purpose; in average year, 2.1 adults/territory (Reid 1971). Each contains tussock, and usually forest and bog; possibly higher than average

soil fertility; water important for drinking, bathing, and wetting food (Williams 1960); correlation between quality of territory and success of breeding (Kean 1956). Each year pair holds same territory; when partner dies, some birds remain in territory, but others move (Williams & Miers 1958; Reid 1967). Estimates of size: 6–18 ha (Williams & Miers 1958); 2–56 ha (Mills 1975); 6–20 ha (DOC in press). Actual area not fixed; boundary expands and contracts; centre may change when chicks become mobile, and as young grow. Interactions between neighbours affect size of territory and of neutral area between neighbouring territories; when birds meet each other in neutral area, status at least partially depends on distance of each from centre of their territory and stage of breeding cycle of each bird (Reid 1977). New territories rarely established on ground already occupied (Williams 1960). By Mar., after breeding, territories enlarge, overlap, and merge into semi-communal home-ranges (Reid 1967); birds range across nearby territories without much friction; possibly, once juveniles independent, territory no longer defended (Reid 1967). **Home-range** In winter possibly range farther than at other times, over c. 200 ha (Williams & Miers 1958; B. Lee); usually occupy grassland and scrub or, if food scarce, forest; some may move to lower altitudes, occupying scrub-grassland above tree-line till thaw (Reid 1967; Mills 1975; Mills *et al.* 1984).

Roosting Under shelter of tussock, scrub, large overhanging rocks; site often used only once, wherever birds happen to be at nightfall. Some sites appear to be used regularly, especially dry sheltered spots. Pairs roost standing next to each other (D. Eason). Pair with chick roosted in same place on two successive nights, and were observed on two other nights in different places (Riney & Miers 1956). Active during day, but also at night (e.g. Williams 1960). Brood-nests built to shelter chicks at night and during bad weather (Reid 1967).

SOCIAL BEHAVIOUR Not well known; based mainly on Falla (1951), Williams (1960), and contribution by G. Rasch and J.A. Mills. Difficult to observe because wary and inhabit thick vegetation in isolated areas. Behavioural sequences easily disrupted by disturbance (Reid 1969a). Some aspects of behaviour similar to those of Purple Swamphen. When moulting, Feb.–Mar., quiet and secretive, and shelter in cliffs or bushes; regularly stand plucking loose feathers; sunbathe with wings spread; bathe in tarns (Fleming 1951; Williams 1960; D. Eason). **GAPING BEHAVIOUR:** bird raises head and opens bill wide with no sound; may continue for some time; often occurs after sleep and always during and after bathing (Williams 1960; D. Eason).

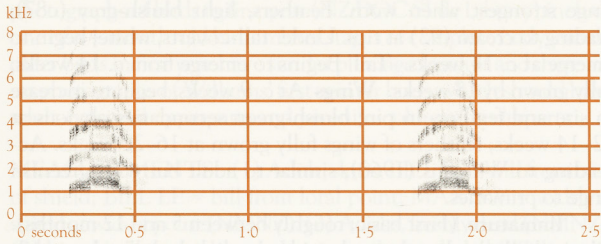
Agonistic behaviour Territorial disputes and fighting occur spring and early summer, as breeding approaches; little conflict during non-breeding season. Intruders usually chased away before fighting begins (Lavers & Mills 1984). **Threat** Before or during conspecific attack, resident rushes at intruder in erect posture with wings held high and arched, neck feathers ruffled, and wing-coverts prominent; indicates extreme threat; also used against avian predators such as Wekas and New Zealand Falcons *Falco novaeseelandiae*. **Fighting** Strike with feet, bill and neck; males fight males, and females fight females; can result in wounds and loss of feathers. **Alarm** Flick tail continuously and rhythmically upwards; birds run into cover in different directions with heads and necks low; often hide till predator very close; one seen diving in stream holding vegetation on bottom with feet (Williams 1960). Carefully watch harriers and other flying birds when some distance away, then slink away and hide if it approaches too close (D. Eason). If captured or surprised at close quarters give screaming distress call and struggle (Hutton & Drummond 1904) (see Relations within family group).

Sexual behaviour Pair-formation Male raises wings close to body with neck erect, and tail lifted and fanned to display white vent; will also stand erect, hunch nape, bend head down, and fan wings out, so that primaries trail on ground; this shows bright feathers of upperparts (G. Rasch). Other mutual displays: when mate called, incubating bird ran crouching to it; birds faced each other with bills almost touching and necks upstretched; position held for several seconds, then one bird crouched, drooped wings, fluffed out feathers of flanks, and moved round partner so that white under tail-coverts prominent (Falla 1951). Similar display, with mutual nibbling, between mated birds that had not yet bred; probably precursor to copulation (Williams 1960). Birds come toward each other with arched wings, then quickly straighten up with bills touching and necks outstretched; often seen before pair copulate (Lavers & Mills 1984). **Greeting** Pairs remain in constant contact by sight and sound; sometimes duet (G. Rasch; J.A. Mills). **Allopreening** Regularly seen between any birds living together: pairs, chicks, and adults and chicks; one preens other's face and chin; bird being preened stretches and twists head upside down. **Copulation** When attempting to mount female, male at first places foot on female's back, and fans and depresses tail; female crouches but remains standing.

Relations within family group During incubation, change-over occurs at nest and eggs rarely unattended. After one egg has hatched, parents occasionally desert remaining egg but more often remain at nest for 3–5 days with young chick. Downy young brooded at night, and during bad weather in brood-nest. Young beg for food, reach up and pluck it from bill of parent (Fleming 1951). Parents and chicks give contact calls to each other; chicks develop adult calls at c. 4.5 months (Fleming 1951; Williams 1960). In captivity, hand-reared chicks imprinted on people and bantams (Reid 1977). **Anti-predator responses of young** Young chicks hide by burrowing into thick grass and remaining silent; lie immobile with head in vegetation until parent signals (Reid 1967); chicks more than 6 months old tend to run. Brooding adult and chick flee from nest (Falla 1949); may give screaming distress call (Hutton & Drummond 1904); Alarm call develops at c. 7 months (Williams 1960). **Parental anti-predator strategies** Incubating bird covers itself with surrounding vegetation; often responds to close predator by slowly tucking head out of sight. When entering and leaving nest, makes use of all cover (Falla 1951). If threatened at nest, some birds hiss, scream and bite rather than leave eggs (D. Eason). If separated from chicks, adults make direct line to them (Fleming 1951). When chicks in danger, Alarm call warns them to remain in cover; quieter version recalls chicks. Many yearlings forced out of natal territory after spring.

VOICE No detailed studies. Hearing the unfamiliar cry was first evidence of continued existence (Falla 1949). Calls include almost monosyllabic *kloup*, low resonant *oomp*, and clucking. Contact Call occasionally heard at night (Williams 1960). Members of pair remain in constant contact by sight or sound (Fleming 1951). Antiphonal duetting follows disturbance by intruder or separation (J.A. Mills); duets use contact call (Fleming 1951). Contact call similar to that of Weka, call of which is disyllabic and more flute-like; Alarm Note also similar to that of Weka, which is more staccato, continuous and frequent; Takahē often answers Weka (Williams 1960) and will respond aggressively to their calls, especially when breeding; often respond to calls of kiwis at night.

Adult Account follows Williams (1960). **CONTACT CALL:** almost monosyllabic *kloup* (sonagram A). Uttered by birds of a pair if separated, or in a territorial dispute conducted at a distance; also to keep contact with a chick (Fleming 1951). **ALARM NOTE:** low and resonant *boomp* (Falla 1949) or percussive *oomp*, described in



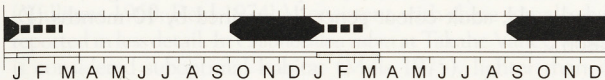
A: J. Kendrick; P100

Maori tradition as sounding like knocking two pieces of greenstone together underwater; repeated slowly and in a rather low tone (Oliver), not easily heard unless close (Turbott 1951). Heard when birds aware of observer, also warns chicks to remain in cover. Quieter version used between pair when close together and undisturbed; with soft rhythmical *kau* superimposed, serves as recall note for chicks. **CLUCKING**: varied, made when feeding undisturbed. **HISS, LOUD SCREECH**: given rarely, when suddenly alarmed at close quarters, threatened, chased or caught (D. Eason).

Young Peeping of chick in unpipped egg audible at 1–3 m (Williams 1960). From chick in black down, cheep in answer to adult Contact Calls (Falla 1951). Fairly constant cry at 6 weeks: either slow *wee-a* or continuous repeated *weedle-weedle-weedle* (Fleming 1951). Continuous hoarse whistle (bass version of juvenile cheep) from chick thought to be aged 3–4 months, three-quarters adult size (Williams 1951). Screaming distress call if captured, repeated *chi-ching*. Adult Contact Call develops at about 4.5 months and Alarm Note at about 7 months (Williams 1960). Young chicks can produce a higher-pitched, quieter version of adult antiphonal duet; this call fully developed by c. 7 months (D. Eason).

BREEDING Monogamous; breed in family groups; first-year birds may assist with incubation and care of young. Based on contribution by G. Rasch and J.A. Mills, and studies by Falla (1951) and Williams (1957, 1960) and DOC (in press).

Season Laying, early Oct. to late Dec., but eggs in nests as late as mid-Feb. and small young found in late Mar. probably result of re-nesting after failure (Williams 1957; D. Eason).



Site In well-drained sites; under or between tussocks of *Chionochloa rubra* and *C. rigida amara* or shrubs such as *Dracophyllum* (Williams 1960; DOC in press). Typically has two entrances, front and back, which connect with runways (Williams 1960; Oliver). Nests have a latrine nearby (Falla 1951). If re-nesting, build new nest (Williams 1960; D. Eason).

Nest, Materials Deep bowl, 76–152 mm height; 31–38 cm diameter and 76 mm thick in centre (Williams 1960). Probably make saucer-like scrape in ground, then construct bowl of fine grasses and tussock leaves. In captivity, both sexes collect material and build nest but female mainly constructs bowl (Williams 1960). May build many trial nests before laying. Construct brood-nests after young leave nest (Williams 1960), 2–5 days after hatching.

Eggs Elliptical, rounded, nearly same at both ends; pale-buff ground-colour with irregular blotches of mauve and brown, not closely spaced (Williams 1960; Oliver). **MEASUREMENTS** (mm): 73.5 (68.3–78.9; 87) x 48.7 (46.1–51.0) (Eason 1992); 73.5 (68–78;

24) x 49.0 (47.5–52.5) (Williams 1960). **WEIGHT**: 96.5 (81.3–109.9; 87) (Eason 1992).

Clutch-size One to three, but usually two eggs (DOC in press); average, 1.7: C/1 x 16, C/2 x 30, C/3 x 2.

Laying Interval between eggs of two-egg clutch, c. 48 h (Williams 1960); in captivity, up to 72 h between second and third egg of C/3 (Eason 1992). Usually only one brood raised per year; second brood once recorded (Williams 1957). If clutch or brood lost, replacement clutches often laid, usually 2–4 weeks later; replacement more common in years when tussock flowered.

Incubation Begins after laying of first egg; hatching interval, c. 48 h (Williams 1960). Both sexes incubate, female usually throughout morning and early afternoon and male for rest of day; eggs never left unattended. Male may also incubate at night. Juveniles, if present in family group, may help incubate but contribution small. Sitting bird may rearrange vegetation within reach to improve concealment (Williams 1960). Pairs sometimes incubate empty nests; one pair for up to 7–8 weeks (Williams 1960). **INCUBATION PERIOD**: 30 days (29–31) (Lavers & Mills 1984; Eason 1992); c. 28 days (Williams 1960) too short. One clutch of infertile or added eggs incubated for c. 54 days before eggs removed; one bird sat on empty nest for another day before leaving area (Falla 1951). Weight loss during incubation, 18.1% over 30 days (n=16) (Eason 1992).

Young Precocial, nidifugous; usually leave nest soon after hatching but may remain in nest for up to 5 days. Active soon after hatching. Chick <1 week old: down, black; bill, black at base with terminal two-thirds, including egg-tooth, ivory-white; legs, purplish brown (Falla 1951). In older chicks, white reduced to small subterminal patch, then disappears (Falla 1951). Down begins to be replaced by juvenile plumage at 1 month (Mills 1974a). **Growth** Weights (g) of chicks reared by parents from Murchison Mts (n=14), Burwood Bush (3) and Tiritiri Matangi I. (1), with no supplementary feeding: hatching, 61 (4.4; 10); Week 1, 81 (21.3; 6); Week 2, 125 (46.5; 10); Week 3, 285 (66.0; 5); Week 4, 444 (96.4; 3); Week 5, 634 (88.7; 5); Week 6, 799 (107.2; 5); Week 7, 894 (42.1; 4); Week 8, 1090 (112.2; 5); Week 9, 1283 (153.6; 4); Week 10, 1400 (76.6; 5); Week 14, 1890 (219.8; 4) (G. Rasch). **Legs and feet** attain adult size by c. 3 months old (G. Rasch). **Parental care, Role of sexes** Both sexes help to rear chick. Parents feed chick by picking up item with bill and passing it to chick, or collecting item from other parent and passing it on (Williams 1960). Chick depends on parents for bulk of food for c. 4 months after hatching. Yearlings in family group help to feed chicks, often taking a major role. Downy young brooded by an adult at night or during bad weather, on any available nest (Falla 1951; D. Eason). Chicks will hide by burrowing into thick grass and remaining silent (Falla 1951).

Fledging to maturity Young remain in family groups through their first winter. Capable of breeding in first year (D. Crouchley *contra* Williams & Miers 1958; Reid 1967).

Success Hatching success from 46 nests, 67–76%; of 37 pairs that hatched chicks, 17 still had a chick alive at c. 3–4 months. From 21 eggs laid (n=12), 12 hatched; from 42 pairs, 21 recently hatched chicks observed, i.e. minimum 0.5 young per pair (Williams 1960). From 36 pairs, including four pairs that incubated empty nests, 15 chicks left the nest, i.e. 0.42 chicks per pair (Williams 1957). Average productivity per breeding pair: 1.78 eggs laid, 0.97 chicks hatched, 0.88 chicks survived to c. 6 weeks old (Reid 1967). On occasions, after first chick hatches and leaves nest, remaining egg deserted or even destroyed (Williams 1960). Survival of seven banded chicks: one not seen again, last sighting of others at 1 week, 2, 11, 12, 13 and 63 months (Williams 1960). Usually one chick raised to independence. Eggs

and chicks taken by stoats and Wekas (Lavers & Mills 1984; Oliver); however, on Kapiti I., no recorded predation of eggs or chicks (R. Empson). Mortality estimate of juveniles over winter for one season, 46%.

PLUMAGES Prepared by D.I. Rogers.

Adult Attained at 1 year. **Head and neck** Uniform dark blue-purple (74), taking on a dull-black (c82) tinge with wear. Feathers have blue-purple (74) tips that have a slight and patchy blue (69) tinge when fresh, and narrow with wear to expose dark-grey (82–83) rest of feathers. **Upperparts** Mantle, glossy blue-purple (74) with concealed dark-grey (82–83) bases to feathers. Back and scapulars look olive, with varying blue iridescence most obvious when backlit and when plumage fresh. Feathers olive (c46) with concealed grey (c84) bases; at junction of these two areas (c. 2 cm from tip of feather), a varying indigo (74) bar, indistinct and tending to be wider towards mantle. Feathers have narrow iridescent light bluish-green tips. Lowermost back, rump and upper tail-coverts, olive (c46) with grey (84) bases. **Underparts** Under tail-coverts, white. Axillaries and feathers at sides of upper breast, as upper back. Rest of underparts, dark blue-purple (74), varyingly tinged dark grey (especially at vent) by concealed dark-grey (83) bases to feathers. **Tail** Olive, slightly darker and bluer than rump and upper tail-coverts. **Upperwing** Primaries, primary coverts, alula, outer secondaries and outer greater secondary coverts have dark blue-purple (74) tips, outer webs and inner edge of inner web; rest of inner web dark brownish-grey (c83) and generally concealed. Inner secondaries and their coverts similar but with lighter growth-bars that show olive or light bluish-green iridescence in some lights. Median, lesser and marginal coverts, dark blue-purple (74) grading to dark-grey (c83) bases; some (especially inner feathers) have light-blue (69) iridescence at tips. **Underwing** Dark grey (83), coverts appearing mottled by their narrow blue-purple (74) tips. Tips of a few coverts have trace of light blue-green iridescence.

Downy young When young, covered in short black (89) down, generally thick but sparse on forehead, and leading-edge of metacarpus bare and conspicuous for c. 8 weeks. Black (89) strands of down grade to dark-brown (c21) bases, which are slightly exposed on centre of belly, thighs and throat. When c. 4 weeks old, down begins to fade and abrade, birds becoming largely black-brown (21); last areas to lose black (at c. 4 weeks) are crown and back. Face, ear-coverts, throat and breast fade paler than rest of downy plumage, becoming light brown (39), buff (124) or whitish. Grey second down develops at 4–5 weeks. Two specimens that died at c. 5 weeks (NMNZ) were apparently developing second down, coloured like the first, on scapulars, flanks and wings.

Juvenile At 5 weeks, grey ear-coverts and indigo feathers of breast begin to emerge; short creamish-buff feathers on vent and abdomen. By 8 weeks, covered in short feathers except on tail, white under tail-coverts and wing; the wing is still small and remains downy and the metacarpus is still bare. **Head and neck** From 8 weeks, neck and top of head, brownish grey (greyish 28). Chin, throat and face similar but feathers have white bases that can be well exposed and make these areas look white varyingly mottled greyish brown. **Upperparts** Olive (43), without iridescence and attaining brown (light 28) tinge with wear; feathers have concealed dark brownish-grey (c84) bases. **Underparts** Breast and upper flanks, dull purplish-blue (c73); when fresh, impression of dullness reinforced by narrow and sparse pale-brown (119D) tips to all feathers. Feathers have concealed grey (c80) bases; on sides of lower breast some have a light-olive tinge near tip. Lower flanks, thighs and vent, cream (92) with a greyish

tinge strongest when worn. Feathers, light bluish-grey (c87), grading to cream (92) at tips. Under tail-coverts, white; begin to emerge at c. 14 weeks. **Tail** Begins to emerge from c. 14 weeks; fully grown by 18 weeks. **Wings** At c. 9 weeks, begin to increase in size and feathers in pin; bluish-green secondaries obvious at 12–14 weeks; feathers of wings fully grown at 16–20 weeks. According to Williams (1960), similar to adult but with greenish tinge to primaries.

Immature (First basic; roughly between 5 and 12 months). Like juvenile; back and mantle said to be slightly duller than adult (Williams 1960).

BARE PARTS Based on photos (Moon 1988; Brathwaite 1986; NZRD; NZ DOC Slide Library).

Adult Frontal shield and basal fifth of bill, red (13–14). Rest of bill, pinkish red (94, c7) to reddish (c13) with a varying horn-yellow (c92) tinge most often seen on culmen, tomia and immediately in front of nostrils. Pattern of yellow tinge varies with flaking of bill-sheath and cannot be used to identify individual birds (Falla 1951). Iris, brown (223B) to reddish brown (136). Feet and legs, pinkish (c7, c3) to pinkish red (c108B). Claws, grey (84, 87) to dark grey (83). **Downy young** At hatching, tip of bill to nostrils, white. When small: gape and most of bill, white; basal quarter of bill and narrow strip along tomia, black (89); frontal shield, a small projection from base of culmen, black (89) and largely obscured by down; iris, black-brown (119) changing to grey (–); feet and legs, pale pink (c7). Before down lost, extent of black on base of bill increases, with area of white being reduced to small white tip on culmen; egg-tooth remains until c. 4 weeks old; feet and legs become dark purplish-brown. **Juvenile** At first, similar to large downy young, but with small but clearly defined black (89) frontal shield, which fades to grey and then lost at 12–14 weeks. Bill begins to fade to light brown to pink, spreading from gonyes, base of upper tomia and tip of upper mandible; at 3–4 months, while in post-juvenile body-moult, culmen, sides of upper mandible and centre of frontal shield still blackish (c82). **Immature** Adult colour of eye attained by c. 5–6 months. Change of colour of bill, shield, legs and feet not related to sex and varies greatly among individuals. Bill and shield change from 6–8 months, beginning at base of bill and edges of frontal shield; later, bluish cast to pinkish bill, which lasts until at least 12 months old. Legs and feet, mostly dull red (–) or pale brownish-orange (–) at 6 months old; adult colour generally attained by 10 months (D. Eason).

MOULTS **Adult post-breeding** Complete; begins about mid-Jan. and continues throughout Feb. and Mar. (Williams 1960; NZRD). Some overlap of moult and rearing of chicks; in Feb., moulted feathers in territory of adults with half-grown chick, including some in brood-nest (Fleming 1951). Primaries and secondaries (excluding tertials) simultaneous (NMNZ). Said to be secretive and quiet during moult; large numbers of feathers left under shelter of shrubs, tussocks, rocks or beside tarns where birds have rested for long periods preening out old feathers (Fleming 1951; Williams 1960; D. Eason). Most museum skins (all examined died in captivity) have broken outer primaries, apparently bitten off as also reported for *Porphyrio porphyrio* (BWP). **Post-juvenile** All juvenile body-feathers replaced in body-moult at c. 4 months; juvenile remiges retained until complete second pre-basic moult at 1 year, which occurs at the same time as in adults. Williams (1960) reported partial moult soon after fledging into first-winter plumage, new feathers being confined to mantle and back. He may have had records only of early stages of complete body-moult, or confused wear-related fading with moult. Many

photographs of birds in first year (NZ DOC Slide Library) include one of a 4-month-old bird in later stages of complete body-moult; older birds in first year have similar plumage to adult and there are no photographs of Williams' first-winter birds, which should have adult-coloured upperparts and juvenile-coloured underparts.

MEASUREMENTS (1) Adult, skins; BILL BS = bill from base of shield; BILL LP = bill from loreal point; MAX SW = width of shield at widest point (NMNZ). (2) Adults, freshly dead (NMNZ). (3) Live birds, age unknown but juveniles excluded (Williams & Miers 1958). (4) Adults from island populations and Burwood Bush (Eason 1992),

	MALES	FEMALES	
WING	(1) 249.7 (5.03; 245–255; 3) (2) 259.3 (6.65; 250–265; 4)	228.7 (3.06; 226–232; 3) 235.3 (9.23; 230–246; 3)	** *
STHP	(1) 179.3 (8.50; 171–188; 3)	160.0 (3.00; 157–163; 3)	**
TAIL	(1) 121, 122 (2) 119.3 (6.99; 110–126; 4)	110.3 (2.08; 108–122; 3) 116.0 (5.29; 110–120; 3)	ns ns
BILL BS	(1) 86.7 (0.73; 85.7–87.4; 4) (2) 87.1 (2.49; 83.5–89.2; 4) (3) 87.9 (1.60; 86–91; 13) (4) 88.9 (2.40; 84.9–94.9; 19)	79.4 (2.76; 76.8–82.3; 3) 82.3 (1.36; 81.2–83.8; 3) 83.3 (1.78; 81–86; 14) 83.6 (3.37; 77.7–89.8; 18)	** ns ** –
BILL LP	(1) 58.6 (1.04; 57.5–60.0; 4)	55.4 (1.07; 54.0–56.4; 4)	*
BILL D	(4) 52.9 (1.58; 49.7–55.0; 11)	48.1 (1.53; 45.4–50.1; 9)	–
MAX SW	(1) 27.2 (1.72; 26.0–29.7; 4) (4) 29.7 (1.97; 26.5–32.8; 19)	24.0 (0.25; 23.8–24.3; 3) 27.8 (2.23; 25.3–34.1; 17)	* –
TARSUS	(1) 97.4 (3.31; 93.9–101.6; 4) (2) 97.0 (2.70; 93.5–99.6; 4) (4) 97.3 (2.62; 92.6–101.3; 19)	91.7 (3.44; 87.3–95.0; 4) 92.0 (2.92; 88.9–95.6; 4) 90.7 (3.34; 83.9–96.1; 18)	ns ns –
TOE-C	(1) 93.8, 94.3 (2) 95.4 (5.11; 90.7–102.1; 4)	87.4, 92.1 92.2 (3.31; 87.7–95.5; 4)	– ns
TOE	(4) 75.3 (2.39; 71.8–79.8; 19)	71.3 (2.15; 66.6–74.9; 18)	–

Williams & Miers (1958) and Williams (1960) took live adults with bill shorter than 86 mm, and weight less than 2.6 kg to be female, larger birds to be male. Dimensions of bill increase till 1 year old; little growth thereafter (G. Rasch).

WEIGHTS Adults at Takahē Valley: males 2673 (257.9; 2250–3250; 13), females 2268 (193.8; 1850–2600; 14) (Williams & Miers 1958); data collected from Takahē Valley since then (Williams 1960; Reid 1974b) consistent with these samples but reported in less detail. In *Chionochloa rubra* at Takahē Valley, which is considered suboptimal habitat (Mills 1975), lighter than in other parts of the Murchison Mts. In *C. rubra* at Takahē Valley, adults (between 19 Jan. and 31 Mar.): males 2670 (220; 18), females 2360 (180; 13). Adults in *C. pallens*, *C. rigida amara* and *C. crassiuscula* at Eyles-Wisely and Miller Peak (at same time): males 2936 (241.6; 18), females 2555 (204.4; 19) (Mills 1975). Little information on seasonal changes of weight or condition of body at particular weights; adults that have died in captivity include a very thin male of 1615 g, and thin females of 1306 and 1430 g (NMNZ). Three immature birds that died during severe winter (Aug.–Oct. 1992): 1050, 1150 and 1220 g (G. Rasch). Hand-reared, captive and island birds (1987–92): males 3100 (2150–4150; 18), females 2650 (1780–3500; 18) (Eason 1992). Reid (1974b) discussed relations between weight, intake of food and faecal output.

STRUCTURE Wing, short and broad. Because birds tend to break outer primaries, only four wing-formulae available. Ten primaries, p7 and p8 longest; p10 39–41 shorter, p9 10–14, p8 0–4, p7 0–2, p6 2–4, p5 5–7, p4 7–10, p3 11–15, p2 17–23, p1 23–29;

inner and outer primaries about equal in width. About 13 secondaries, including about three tertials. Sharp and fairly robust carpal spur c. 10 mm long, largely concealed by feathers in adults, more conspicuous in small downy young. Tail, short and rounded; ten soft feathers. Bill, massive and laterally compressed; slightly shorter than head, almost as deep at base as it is long; c. 47 mm deep and 24 mm wide at base. Culmen decurves gradually towards sharply pointed tip; tomia are rough and slightly decurved; gonys straight. Frontal shield in adults extends from base of culmen to rear of eye; nostrils, large, circular. Legs and feet, stout and rather short. Tarsus, slightly flattened; scutellate in front and behind with small irregular scales on side. Outer toe c. 82% of middle, inner c. 81%, hind c. 45%. Claws, robust and blunt in populations in rocky alpine habitat; long and sharp in soft soils of lowlands (e.g. on islands and in captivity) (G. Rasch).

GEOGRAPHICAL VARIATION Nominate *mantelli*, known from subfossils in NI, was larger than *hochstetteri*, e.g. tarsus 113–129 (Williams 1960; Scarlett 1972; Ripley 1977).

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Volume 2, Plate 47 [caption error corrected from original]

Takahe *Porphyrio mantelli* (page 593)

1 Adult; 2 Downy young, newly hatched; 3 Juvenile, not fully grown; 4 Worn juvenile in post-juvenile moult

Purple Swamphen *Porphyrio porphyrio* (page 577)

5 Adult, subspecies *melanotus*; 6 Adult, subspecies *bellus*; 7 Newly hatched downy young, subspecies *melanotus*; 8 Large downy young, subspecies *melanotus*; 9 Juvenile, subspecies *melanotus*, not fully grown; 10 Immature, subspecies *melanotus*; 11 Adult, subspecies *melanotus*